



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

A test of the 'one-point method' for estimating maximum carboxylation capacity from field-measured, light-saturated photosynthesis

Citation for published version:

De Kauwe, MG, Lin, YS, Wright, IJ, Medlyn, BE, Crous, KY, Ellsworth, DS, Maire, V, Prentice, IC, Atkin, OK, Rogers, A, Niinemets, U, Serbin, SP, Meir, P, Uddling, J, Togashi, HF, Tarvainen, L, Weerasinghe, LK, Evans, BJ, Ishida, FY & Domingues, TF 2015, 'A test of the 'one-point method' for estimating maximum carboxylation capacity from field-measured, light-saturated photosynthesis' *New Phytologist*. DOI: 10.1111/nph.13815

Digital Object Identifier (DOI):

[10.1111/nph.13815](https://doi.org/10.1111/nph.13815)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

New Phytologist

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



1 **A test of the “one-point method” for estimating maximum carboxylation capacity from**
2 **field-measured, light-saturated photosynthesis**

3
4

5 **Martin G. De Kauwe¹, Yan-Shih Lin¹, Ian J. Wright¹, Belinda E. Medlyn², Kristine Y.**
6 **Crous^{2,3}, David S. Ellsworth², Vincent Maire⁴, I. Colin Prentice^{1,5}, Owen K. Atkin⁶,**
7 **Alistair Rogers⁷, Ülo Niinemets^{8,9}, Shawn Serbin⁷, Patrick Meir^{10,11}, Johan Uddling¹²,**
8 **Henrique F. Togashi^{1,13}, Lasse Tarvainen^{14,15}, Lasantha K. Weerasinghe^{6,16}, Bradley J.**
9 **Evans^{13,17}, F. Yoko Ishida¹⁸ and Tomas F. Domingues¹⁹**

10

11 ¹Macquarie University, Department of Biological Sciences, New South Wales 2109, Australia;
12 ²Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797,
13 Penrith, NSW 2751, Australia; ³ Birmingham Institute of Forest Research, University of
14 Birmingham, Edgbaston B15 2TT, UK ⁴Université du Québec à Trois-Rivières, Trois-Rivières,
15 Québec G9A 5H7, Canada; ⁵AXA Chair of Biosphere and Climate Impacts, Grand Challenges
16 in Ecosystems and the Environment and Grantham Institute – Climate Change and the
17 Environment, Department of Life Sciences, Imperial College London, Silwood Park Campus,
18 Buckhurst Road, Ascot SL5 7PY, UK; ⁶ARC Centre of Excellence in Plant Energy Biology,
19 Research School of Biology, Building 134, The Australian National University, Canberra,
20 ACT 2601, Australia; ⁷Biological, Environmental and Climate Sciences Department,
21 Brookhaven National Laboratory, Upton, NY 11973, USA; ⁸Institute of Agricultural and
22 Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 1, Tartu 51014,
23 Estonia; ⁹Estonian Academy of Sciences, Kohtu 6, 10130 Tallinn, Estonia; ¹⁰Research School
24 of Biology, Australian National University, Canberra, Australia; ¹¹School of Geosciences,
25 University of Edinburgh, United Kingdom; ¹²University of Gothenburg, Department of
26 Biological and Environmental Sciences, P.O. Box 461, SE-40530 Gothenburg, Sweden;
27 ¹³Terrestrial Ecosystem Research Network, Ecosystem Modelling and Scaling Infrastructure,
28 The University of Sydney, NSW 2006; ¹⁴Department of Forest Ecology and Management,
29 Swedish University of Agricultural Sciences (SLU), SE-901 83, Umeå, Sweden; ¹⁵Department
30 of Biological and Environmental Sciences, University of Gothenburg, PO Box 461, SE-405 30
31 Gothenburg, Sweden; ¹⁶Faculty of Agriculture, University of Peradeniya, Peradeniya 20400,
32 Sri Lanka; ¹⁷The University of Sydney, Department of Environmental Sciences, NSW 2006;
33 ¹⁸James Cook University, College of Marine and Environmental Sciences, Centre for Tropical
34 Environmental and Sustainability Science, Cairns, Australia; ¹⁹Universidade de São Paulo,

35 Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Av Bandeirantes, 3900, CEP
36 14040-901, Bairro Monte Alegre, Ribeirão Preto, SP, Brazil.

37

38 Author for correspondence:

39 Martin G. De Kauwe

40 Tel: +61 2 9850 9256

41 Email: mdekauwe@gmail.com

42

43

44 Total word count: 6115/6500 (From Intro to Acknowledgements)

45 Details: Introduction: 1,629; Materials and Methods: 1,285; Results: 1160; Discussion: 1,762

46 (28.8% < 30%); Acknowledgements: 279; Number of figures: 7 (+5 supplementary); Number

47 of coloured figures: 7 (+5 supplementary); Number of tables: 2; Supporting information: 1.

Commented [MD1]: Needs fixing

48

49

50

51

52

53

54

55

56

57

58 **Summary**

- 59 • Simulations of photosynthesis by terrestrial biosphere models typically need a
60 specification of the maximum carboxylation rate (V_{cmax}). Estimating this parameter using
61 A - C_i curves (net photosynthesis, A , vs. intercellular CO_2 concentration, C_i) is laborious,
62 which limits availability of V_{cmax} data. However, many multi-species field data sets
63 include A_{sat} (net photosynthetic rate at saturating irradiance at ambient atmospheric CO_2
64 concentration) measurements, from which V_{cmax} can be extracted using a “one-point
65 method”.
- 66 • We used a global data set of A - C_i curves (564 species from 46 field sites, covering a range
67 of plant functional types) to test the validity of an alternative approach to estimate V_{cmax}
68 from A_{sat} via this “one-point method”.
- 69 • If leaf respiration during the day (R_{day}) is known exactly, V_{cmax} can be estimated with an r^2
70 $= 0.98$ and root mean squared error (RMSE) of $8.19 \mu\text{mol m}^{-2} \text{s}^{-1}$. However, R_{day} typically
71 must be estimated. Estimating R_{day} as 1.5% of V_{cmax} , we found that V_{cmax} could be estimated
72 with an $r^2 = 0.95$ and RMSE of $17.1 \mu\text{mol m}^{-2} \text{s}^{-1}$.
- 73 • The one-point method provides a robust means to expand current databases of field-
74 measured V_{cmax} , giving new potential to improve vegetation models and quantify the
75 environmental drivers of V_{cmax} variation.
- 76 •

77 **Keywords:** V_{cmax} , photosynthesis, one-point method, A_{sat} , A - C_i curve, R_{day} .

78

79

80

81

82

83

84

85

86

87 **Introduction**

88 Photosynthesis is a primary driver of the terrestrial carbon cycle (Prentice *et al.*, 2001; Beer *et al.*, 2010) and accurate modelling of this process is critical for projecting the response of the
89 terrestrial biosphere to environmental change (Friedlingstein *et al.*, 2014). Terrestrial biosphere
90 models (TBMs; including ecosystem, land surface and vegetation models) almost universally
91 simulate photosynthesis following the leaf biochemical model of Farquhar *et al.*, (1980), or a
92 variant of this approach (e.g. Collatz *et al.*, 1991). This approach relies on the accurate
93 estimation of two key model parameters: V_{cmax} , the maximum carboxylation rate, and J_{max} , the
94 maximum rate of electron transport (von Caemmerer, 2000). A third term, triose-phosphate
95 utilisation, is often ignored as it is thought to seldom limit photosynthesis under field conditions
96 (Sharkey *et al.*, 1985; but see Ellsworth *et al.*, 2015). In many cases both V_{cmax} and J_{max} scale
97 linearly with leaf nitrogen (N) (Field & Mooney, 1986; Hirose & Werger 1987), although the
98 scaling with N can differ among biomes (e.g. Meir *et al.*, 2002; Domingues *et al.*, 2015). V_{cmax}
99 and J_{max} also tend to be closely correlated, a fact that some models exploit by assuming J_{max}
100 can be determined through a fixed relationship with V_{cmax} (see Niinemets & Tenhunen (1997)
101 for a critique), or, at least, assuming that variation in the two properties is tightly coordinated
102 (Chen 1993; Maire *et al.*, 2012). Nevertheless, V_{cmax} and J_{max} both vary considerably among
103 species (up to a 30-fold variation; Walker *et al.* 2014; Ali *et al.* 2015), among and within plant
104 functional types (PFTs) (Wullschlegel 1993; Kattge *et al.* 2009; Maire *et al.*, 2012; Ali *et al.*
105 2015), and within individual species. Given this large variability it is perhaps unsurprising that
106 TBMs have demonstrated considerable sensitivity in simulated carbon fluxes due to
107 uncertainty in these parameters (Bonan *et al.*, 2011; Piao *et al.*, 2013). As a consequence these
108 parameters are often used as a method of model “tuning” to obtain more accurate fluxes (which
109 we consider as obtaining the ‘right answer for the wrong reasons’), rather than as a means of
110 characterising a PFT-specific trait (Rogers, 2014).

112

113 Traditionally, the photosynthesis model parameters V_{cmax} and J_{max} have been estimated by
114 fitting the Farquhar *et al.*, (1980) photosynthesis model directly to photosynthetic CO₂ response
115 curves, where photosynthesis is measured at several CO₂ concentrations and under saturating
116 irradiance (net photosynthesis, A ($\mu\text{mol m}^{-2} \text{s}^{-1}$), vs. intercellular CO₂ concentration, C_i (μmol
117 mol^{-1}); so-called A - C_i curves). However, accurately determining these parameters from such
118 measurements is not a straightforward process (see Long & Bernacchi *et al.*, 2003). Firstly, A -

119 C_i data are time consuming to collect: each CO_2 response curve may take an hour to set up and
120 measure, particularly in stressed plants where stomatal closure may even prohibit such
121 measurements. Secondly, a number of competing methods exist for fitting the data (Sharkey
122 *et al.*, 2007; Dubois *et al.*, 2007; Patrick *et al.*, 2009; Gu *et al.*, 2010; Feng & Dietze, 2013)
123 and, depending on the chosen method, parameter estimates may vary even for the same datasets
124 (Miao *et al.*, 2009; Niinemets *et al.*, 2009). Many individual experimental studies tend to focus
125 just on a small number of species and, more often than not, they concern plants grown and
126 measured in controlled environments (laboratory or glasshouse). As a result, compared to many
127 plant traits, there is a general paucity of field-measured V_{cmax} and J_{max} data, which likely
128 undermines the accuracy of model simulations of terrestrial photosynthesis. The largest data
129 compilations to date included V_{cmax} data based on $A-C_i$ curve analysis for 127 species (Ali *et al.*,
130 2015), 114 species (Walker *et al.*, 2014), 130 species (Sun *et al.*, 2014) and 109 species
131 (Wullschlegel 1993), but it is unclear what proportion of these data were for field-grown plants,
132 nor what total species number these represent, with many individual datasets appearing in more
133 than one compilation. Currently in the TRY database (www.try-db.org; accessed 7 July 2015)
134 there are geo-referenced V_{cmax} data for 353 species (of which *c.* 250 were obtained from $A-C_i$
135 curves).

136

137 In contrast to the relatively limited number of field-measured $A-C_i$ curves, there is a plethora
138 of net photosynthesis measurements obtained in the field at ambient $[\text{CO}_2]$ and at saturating
139 irradiance (A_{sat}) – e.g. 1500 species were included in the compilation by Maire *et al.*, (2015;
140 dataset assembled in 2008), the TRY database currently contains geo-referenced
141 photosynthesis data for 2192 species (8522 individual observations), and in recent years there
142 have been a number of large field campaigns, from which the data are yet to make it into these
143 types of databases. Together, these A_{sat} data represent species from large parts of the globe, and
144 all PFTs (Kattge *et al.* 2011), but are currently left out of analyses of V_{cmax} . By virtue of their
145 global coverage, analyses of A_{sat} have included quantification of latitudinal, climate- and soil-
146 related trends, including modulation of relationships between A_{sat} and other leaf traits (Reich
147 *et al.*, 1997, 2009; Wright *et al.* 2005; Ordonez & Olf 2013; Maire *et al.*, 2015). When
148 corresponding values of C_i and leaf temperature are reported with each A_{sat} measurement, and
149 if one assumes: (1) that photosynthesis at saturating irradiance is Rubisco-limited (rather than
150 being limited by RuBP regeneration); and (2) that the value of leaf mitochondrial respiration
151 in the light (i.e. ‘day’ respiration, R_{day}) can be estimated, then the V_{cmax} value required to

152 support the observed rate of A_{sat} can be estimated. This estimated quantity is hereafter referred
153 to as \hat{V}_{cmax} , and the method as the “one-point method” (Wilson *et al* 2000). However, whether
154 A_{sat} -dependent estimates of \hat{V}_{cmax} are an accurate reflection of the V_{cmax} values obtained from
155 full $A-C_i$ curves remains uncertain. In the absence of measurements of C_i , values may be
156 estimated from data reported for stomatal conductance and ambient $[\text{CO}_2]$. Values for R_{day} may
157 be estimated from either a relationship with dark respiration, R_{dark} , or by assuming a
158 relationship with V_{cmax} ; see below).

159

160 Although several studies have indeed done this – used measurements of A_{sat} and associated
161 parameters to estimate \hat{V}_{cmax} (Niinemets *et al.*, 1999; Wilson *et al.*, 2000; Kosugi *et al.*, 2003;
162 Grassi *et al.*, 2005; Kattge *et al.*, 2009; Uddling *et al.*, 2009; Niinemets *et al.*, 2015) – a
163 thorough examination of the issues associated with this approach has not been made. That said,
164 preliminary tests of the approach were encouraging. For five tree and five understory species
165 Wilson *et al.*, (2000) estimated V_{cmax} from $A-C_i$ curves as well as from independent
166 measurements of the assimilation rate, C_i at the ambient external CO_2 concentration ($360 \mu\text{mol}$
167 mol^{-1}) and a constant value of R_{day} ($\sim 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$). The two sets of estimates were tightly
168 correlated ($r^2 = 0.97$) with an intercept not statistically different from zero, but with a small
169 bias in the slope (1.08). Grassi *et al.*, (2005) demonstrated that this method could be used to
170 accurately estimate V_{cmax} for three deciduous forest species ($r^2 = 0.97$; slope = 0.96). Given the
171 global coverage of A_{sat} data, there could be great potential for deriving \hat{V}_{cmax} from datasets such
172 as that of Maire *et al.* (2015), or the TRY database (Kattge *et al.*, 2011), providing a means to
173 dramatically expand the species- and geographic coverage of V_{cmax} estimates from field-grown
174 plants in global databases. Nevertheless, employing this approach may result in errors and/or
175 bias, which leads to the question and the focus of this study: “*How robust is the so-called one-*
176 *point method for estimating V_{cmax} ?*” Errors in estimation are principally likely to occur if (1)
177 the biochemical limitation to A_{sat} is not Rubisco activity or (2) if the estimate of R_{day} is biased
178 (Figure 1).

179

180 We tested how well the one-point method works, by estimating V_{cmax} from complete $A-C_i$
181 response curves and comparing these values with V_{cmax} estimated using the one-point method
182 applied to the A_{sat} data extracted from these curves. To this end, we compiled 1,394 $A-C_i$

183 response curves, from 564 species. These data represent by far the largest compilation of field-
184 measured photosynthetic CO₂-response data to date. These data are taken from all vegetated
185 continents – from the Arctic to the tropics – and so represent a broad spread of site climates
186 (Fig S1). Using this dataset, we sought to test the following hypotheses:

- 187 i. That under ambient CO₂ and saturating irradiance, A_{sat} is normally Rubisco-limited, or
188 co-limited by Rubisco and electron transport (a requirement for the one-point method
189 to be valid). There are environmental conditions where this is less likely to be true,
190 leading to the following additional hypotheses:
- 191 a. In mesophytic leaves growing in wet and/or humid environments, the effective
192 operational C_i for leaves is likely to be high, meaning, the leaf is more likely to
193 be electron-transport limited, and thus \hat{V}_{cmax} values are more likely to be
194 underestimated.
- 195 b. The J_{max} to V_{cmax} ratio at 25 °C has been found to decline with increasing growth
196 temperature (Dreyer *et al.* 2001; Medlyn *et al.*, 2002a; Kattge & Knorr, 2007;
197 Lin *et al.*, 2013). As a result, the leaf is more likely to be electron-transport
198 limited at higher growth temperatures; thus we also hypothesise an under-
199 estimation of V_{cmax} at higher growth temperatures.
- 200 ii. Estimates of V_{cmax} would in general be less accurate for leaves operating at low A_{sat}
201 and/or low g_s because the cumulative effect of errors in the various underlying
202 assumptions would contribute to a lower signal-to-noise ratio.
- 203 iii. Uncertainties in R_{day} can contribute to greater bias for estimating V_{cmax} using the one-
204 point method.

205 In this study we provide a thorough analysis of the one-point method for estimating
206 carboxylation capacity from point measurements of light-saturated photosynthesis, and
207 indicate the conditions under which it works best or may be subject to greater errors. Our
208 primary purpose is to find out whether it would be viable to markedly expand plant trait
209 databases of maximum carboxylation capacity, V_{cmax} , by supplementing those data acquired
210 from A - C_i curves with values derived from A_{sat} by the one-point method.

211

212

213

Commented [MD2]: Find ref.

214 **Material and Methods**

215 *Datasets*

216 We collated 1,394 $A-C_i$ curve measurements from 564 C3 species (91 families) and 46 field
217 sites across various ecosystems, including Arctic tundra, boreal and temperate forest, semi-arid
218 woodlands and tropical forest (Table 1, Figure S1). In most cases measurements were made
219 using the LI-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE, USA), except
220 for one data set obtained in Estonia which was measured using a customised open system
221 (Niinemets *et al.*, 1998). We selected data where measurements were first conducted at ambient
222 CO_2 concentration (360–400 $\mu mol mol^{-1}$, depending on the year of collection) and saturating
223 irradiance conditions (photosynthetic photon flux density, PPFD, between 1000 and 2000 μmol
224 $m^{-2} s^{-1}$). The measurements then progressed through a series of step-wise changes in CO_2
225 concentration spanning sub-ambient (40–400 $\mu mol mol^{-1}$) and super-ambient saturating CO_2
226 concentration (typically $> 700 \mu mol mol^{-1}$). During each $A-C_i$ response curve measurement,
227 leaf temperatures were maintained close to the site ambient temperature, ranging from 6 to
228 40°C. Any measurements obtained which did not follow this protocol, e.g. in cases where the
229 first measurement was recorded at sub-ambient CO_2 , were not used in our analyses.

230

231 *Estimation of apparent V_{cmax} , J_{max} and R_{day} from $A-C_i$ response curves*

232 We first estimated apparent V_{cmax} , J_{max} and R_{day} by fitting each field-measured $A-C_i$ curve using
233 the C₃ photosynthesis model of Farquhar *et al.*, (1980). Several different estimates for the
234 temperature-dependence of K_c , the Michaelis constant for CO_2 ($\mu mol mol^{-1}$), K_o , the Michaelis
235 constant for O_2 ($mmol mol^{-1}$), and I^* , the CO_2 compensation point in the absence of
236 mitochondrial respiration ($\mu mol mol^{-1}$), can be found in the literature (Badger & Collatz, 1977;
237 Jordan & Ogren, 1984; Brooks & Farquhar, 1985, Bernacchi *et al.*, 2001; Crous *et al.*, 2013).
238 We chiefly use values taken from Bernacchi *et al.* (2001), hereafter denoted B01, in common
239 with many TBMs. To test whether the choice of values for these parameters affects the success
240 of the one-point method, we also used two alternative sets of these parameters, namely those
241 advanced by Badger & Collatz (1977) (denoted BC77) and Crous *et al.*, (2013) (denoted C13):
242 see Table 2 for details. The I^* temperature dependencies of tobacco (B01) and eucalypt (C13)
243 represent two extremes of the most and least temperature-sensitive I^* responses respectively,

244 using *in vivo* gas exchange methods (Crous, unpublished data). To contrast with *in vitro*
245 methods, we also considered the temperature response of I^* in *Atriplex glabriuscula* (BC77).

246

247 The intercellular concentration of oxygen (O_i) was assumed to be 210 mmol mol⁻¹ for all data
248 collected at sea level. In other datasets, O_i , C_i , and I^* were corrected for the effect of elevation
249 on partial pressure by multiplying by the observed pressure readings and correcting units to
250 μ bar, mbar and mbar, respectively. For calculations with the B01 and C13 temperature
251 dependencies, K_o and K_c were converted to units of μ bar and mbar, respectively. This was done
252 by assuming that the original measurements were obtained at an average atmospheric pressure
253 of 987 mbar in Urbana, Illinois (von Caemmerer *et al.*, 2009). K_o and K_c values from BC77
254 were simply converted from concentration to partial pressures assuming a standard pressure of
255 1011.35 mbar.

256

257 We assumed an infinite mesophyll conductance (g_m); therefore the estimated V_{cmax} and J_{max}
258 values should be regarded as *apparent* values (Evans 1986; Sun *et al.*, 2013), as generally used
259 in TBMs and reported in most of the ecophysiological literature. A closer match to *in vitro*
260 enzyme activity of Rubisco can be obtained by considering the mesophyll conductance to CO₂
261 to the sites of carboxylation (Flexas *et al.*, 2007; Rogers *et al.*, 2001); however, as g_m values
262 are available for so few of the sampled species, we assumed that C_i is equal to C_c , the CO₂
263 concentration at the chloroplast. The C_i at which photosynthesis is co-limited by both
264 carboxylation and RuBP regeneration was calculated for each $A-C_i$ curve based on the apparent
265 V_{cmax} , J_{max} and R_{day} using the C₃ photosynthesis model. As the temperature responses of V_{cmax} ,
266 J_{max} and R_{day} are not the focus of our study, we did not adjust the estimated parameter values
267 to a standard temperature. Therefore, all the parameters were estimated at their corresponding
268 measured leaf temperatures. All parameter fits were carried out using the Levenberg–
269 Marquardt least squares approach (Levenberg, 1944; Marquardt, 1963); the source code is
270 freely available from GitHub (De Kauwe *et al.* 2015). Of the 1,394 measured $A-C_i$ curves, the
271 data used to estimate V_{cmax} were screened to exclude “bad” measurement curves based on the
272 traditional $A-C_i$ fitting approach, “bad” being defined as: (i) if the first obtained measurement
273 was at an ambient CO₂ concentration < 300 or > 400 μ mol mol⁻¹; (ii) if the fitted function had
274 $r^2 < 0.9$; or (iii) if the relative error of fitted V_{cmax} values is > 40%. After screening this resulted
275 in 1318 measurements; filtering criteria (i), (ii) and (iii) removed ~4%, 1% and 1%,

276 respectively The fitting method used makes no assumption about the C_i value at which the leaf
 277 transitions between carboxylation and RuBP regeneration limitations (C_i transition point), but
 278 it does use a hyperbolic minimum function to smooth the transition between the carboxylation
 279 and RuBP regeneration limitations (Kirschbaum & Farquhar, 1984).

280

281 \hat{V}_{cmax} estimation from the one-point method

282 The main underlying assumption of the one-point method is that leaf net photosynthesis under
 283 ambient CO_2 and saturated irradiance conditions is limited by Rubisco carboxylation rather
 284 than by RuBP regeneration (Wilson *et al.*, 2000; Rogers & Humphries, 2000). As such, \hat{V}_{cmax}
 285 can be estimated from the carboxylation-limited portion of the photosynthetic- CO_2 response
 286 curve, given by:

$$\hat{V}_{\text{cmax}} = (A_{\text{sat}} + R_{\text{day}}) \frac{(C_i + K_m)}{(C_i - \Gamma^*)} \quad (1)$$

287 where K_m is the Michaelis-Menten constant, given by:

$$K_m = K_c \left(1 + \frac{O_i}{K_o} \right) \quad (2)$$

288 K_c , K_o (and Γ^*) were estimated following the equations in Table 2. We used the first
 289 measurement point of each A - C_i curve as the A_{sat} value required to estimate V_{cmax} . One difficulty
 290 with this approach is that it requires an estimate of R_{day} . In the first instance we used the fitted
 291 value for R_{day} obtained from the A - C_i curve (hereafter called ‘known’ R_{day}). This approach may
 292 be viewed as a “best-case” test of the method, since these values will not be known when only
 293 A_{sat} is measured. In order to estimate V_{cmax} in the situation where R_{day} is not known, we assumed
 294 that R_{day} was 1.5% of V_{cmax} (hereafter called ‘estimated’ R_{day}), following Collatz *et al.*, (1991).
 295 Under this assumption, the estimation equation is:

$$\hat{V}_{\text{cmax}} = A_{\text{sat}} \left(\frac{C_i + K_m}{C_i - \Gamma^*} - 0.015 \right) \quad (3)$$

296 The fixed proportion between R_{day} and V_{cmax} was proposed by Collatz *et al.* (1991) to hold at
 297 25°C. We further assumed that this ratio would remain constant with varying leaf temperature,
 298 thus assuming similar temperature dependences for R_{day} and V_{cmax} . This assumption is
 299 reasonable because leaf respiration and V_{cmax} both typically have increasing temperature

300 dependences with Q10 values close to 2 at temperatures up to 35°C (Collatz *et al.*, 1991;
301 Medlyn *et al.*, 2002; Atkin *et al.*, 2015).

302

303 *Assessing the robustness of the one-point method*

304 We compared \hat{V}_{cmax} values to V_{cmax} values estimated from each full $A-C_i$ curve in order to
305 assess the performance of the one-point method. We also analysed the residuals as a function
306 of a range of variables to identify the circumstances under which the method is most (or least)
307 successful.

308

309 As there were 1318 data points we opted in a number of comparison plots to (i) group (colour)
310 species by PFT and also (ii) to bin these data (Fig. 2, 4, 5, 7, S1 and S2). Binning the data (with
311 all values within a ‘bin’ being averaged out to a single value), allows us to better visualise the
312 underlying main trends in large datasets, rather than being distracted by the small number of
313 points towards the edges of any bivariate distribution. Regression lines however were fitted to
314 raw data, not to the binned data. Bin sizes are shown in all figure captions.

315

316 *Other datasets*

317 Using 0.5° resolution Climate Research Unit climatology data (CRU CL1.0; New *et al.* 1999)
318 over the period 1961 to 1990, we derived for each site: mean annual temperature (MAT; a
319 proxy for growth temperature); mean annual precipitation (MAP); a moisture index
320 (representing an indirect estimate of plant water availability, calculated as the ratio of mean
321 annual precipitation to the equilibrium evapotranspiration as described in Gallego-Sala *et al.*,
322 2010); and the number of growing degree days above 0 and 5 degrees C, respectively. We also
323 obtained site elevation estimates from data from the Advanced Spaceborne Thermal Emission
324 and Reflection Radiometer (ASTER) Global Digital Elevation Model Version 2 (GDEM V2)
325 at 1.0° resolution.

326

327 **Results**

328 The C_i transition point of each $A-C_i$ curve was located by fitting both the Rubisco-limited and
329 RuBP-limited net CO_2 assimilation rates and then identifying the point at which the two
330 limitations intersected (transition point) (Fig. 2a). In our dataset *c.* 94 % of the measured A_{sat}
331 values were found to be Rubisco-limited under saturated irradiance and ambient CO_2 . This
332 result supports the key underlying assumption of the one-point approach: that in field datasets
333 at current C_a and (importantly) at light saturation, carboxylation usually limits A (hypothesis i).
334 Among the wide range in estimated transition points there was some distinct patterning
335 according to plant functional type (PFT; Fig 2b); namely, higher median transition points for
336 evergreen needleleaf species than in broadleaf species (whether evergreen or deciduous; post
337 hoc Tukey tests: $p < 0.001$), and higher median transition points in herbaceous species than in
338 deciduous shrubs (post hoc Tukey test: $p = 0.08$) (note the deciduous needleleaf forests PFT
339 only has three sample curves).

340

341 *Known R_{day}*

342 When R_{day} was known, \hat{V}_{cmax} values were in excellent agreement with V_{cmax} derived from
343 traditional $A-C_i$ curve fitting (Fig. 3). Across all species, \hat{V}_{cmax} values were estimated with a
344 positive bias of $0.99 \mu\text{mol m}^{-2} \text{s}^{-1}$; $r^2 = 0.98$; root mean squared error (RMSE) = $8.19 \mu\text{mol m}^{-2} \text{s}^{-1}$.
345 Error and bias varied somewhat among PFTs (bias = $-4.02 - -2.26 \mu\text{mol m}^{-2} \text{s}^{-1}$; $r^2 > 0.95$;
346 RMSE: $4.33 - 10.34 \mu\text{mol m}^{-2} \text{s}^{-1}$) but were still rather modest even in the worst case,
347 deciduous shrubs (RMSE = $10.34 \mu\text{mol m}^{-2} \text{s}^{-1}$).

348

349 Residuals between V_{cmax} and \hat{V}_{cmax} were examined as a function of several factors, namely:
350 V_{cmax} estimated from traditional $A-C_i$ curves (Fig. 4a), ambient g_s (Fig. 4c), estimated R_{day} (via
351 $A-C_i$ curve; Fig. 4e) and ambient C_i (Fig. 4g); leaf temperature, mean annual temperature (MAT;
352 a proxy for growth temperature) and mean annual precipitation (MAP) (Fig. 5); and a selection
353 of other common indices of site climate (site moisture index, elevation, growing degree days;
354 Figs. S2-3). The plot of residuals against the “true” V_{cmax} values (Fig. 4a) shows considerable
355 scatter in individual \hat{V}_{cmax} values. When using a known R_{day} , this spread in errors largely
356 disappears in the binned data, suggesting that it results from a small number of individual
357 measurements. There was a positive trend in the residuals that indicates increasing error with

358 increasing V_{cmax} values, but importantly, most (~10 % of binned data) errors are small (within
359 10%, denoted by dotted lines in Fig. 4a).

360

361 We originally hypothesised that we would observe larger biases between \hat{V}_{cmax} and V_{cmax} at
362 high ambient C_i and in species sampled from very wet and/or humid environments, due to a
363 greater stomatal aperture (hypothesis i(a)). When using a known R_{day} our dataset did not support
364 this hypothesis (Fig 4c): at high g_s , there was a weak trend for over-estimation of V_{cmax} , rather
365 than the hypothesised under-estimation expected if the error resulted from being above the
366 operating C_i . Whilst there was a small trend with MAP, the slope was negligible (Fig. 5c) and
367 there were no trends when examining the residuals as a function of C_i (Fig. 4g). We also
368 hypothesised that we might see greater bias at high growth temperatures (hypothesis i(b)).
369 When using a known R_{day} , our results do indeed show a significant trend with increasing MAT
370 (proxy for growth temperature; Fig 5c), and the annual number of growing degree-days (Fig.
371 S3), but again the slope of this trend was negligible. We also hypothesised that we may see
372 larger error (both absolute and relative) in the residuals at low g_s values due to a low signal-to-
373 noise ratio (hypothesis ii). To test this prediction, we divided the measurements into two groups:
374 those at low g_s ($<0.2 \text{ mol m}^{-2} \text{ s}^{-1}$) and those at higher g_s ($>0.2 \text{ mol m}^{-2} \text{ s}^{-1}$). The RMSE was
375 similar in both groups ($8.07 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ vs. $8.37 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ at low and high g_s , respectively),
376 but the percentage error was greater (8.4% vs. 4.5%), supporting our prediction.

377

378 *Estimated R_{day}*

379 Errors were noticeably greater when R_{day} was estimated as a fixed fraction of V_{cmax} . Overall
380 (all species) there was a negative bias: $-2.2 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$; $r^2 = 0.95$; RMSE: $17.1 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$.
381 When grouping by PFT these errors increased further (biases $-8.18 - 10.93 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$; $r^2 >$
382 0.85 ; RMSE: $8.30 - 26.46 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$). Examining the residuals between V_{cmax} and \hat{V}_{cmax} as
383 a function of the “true” V_{cmax} values (Fig. 4b) showed a negative trend suggesting an over-
384 estimation of V_{cmax} at higher values. Errors were greatest for species grouped into the deciduous
385 broadleaf forest PFT; here \hat{V}_{cmax} values are systematic over-estimates.

386

387 These results provide strong support for the hypothesis that uncertainties in R_{day} would
388 contribute to bias in estimating V_{cmax} values (hypothesis iii). Overall, errors were greater across
389 all comparisons when using an estimated R_{day} compared to errors with a known R_{day} .
390 \hat{V}_{cmax} values also showed a positive trend with increasing R_{day} (Fig. 4f), suggesting a modest
391 but systematic under-estimation of \hat{V}_{cmax} at R_{day} values $< 2 \mu\text{mol m}^{-2} \text{s}^{-1}$, and an over-estimation
392 at higher R_{day} values.

393

394 To enable the estimation of V_{cmax} without an independent estimate of R_{day} , we assumed a fixed
395 relationship with V_{cmax} that is commonly used in TBMs. However, there was a strong negative
396 relationship between $V_{\text{cmax}} - \hat{V}_{\text{cmax}}$ residuals and leaf temperature (Fig. 5b) and a notable
397 positive trend in errors with increasing estimates of R_{day} (Fig. 4f), both of which suggest that
398 the relationship between R_{day} and V_{cmax} is not constant. Figure 6a shows the $R_{\text{day}}:V_{\text{cmax}}$ ratio
399 obtained from fitting our $A-C_i$ response curves as a function of leaf temperature for the B01
400 temperature dependencies for K_c , K_o and I^* . The data show a strong negative trend with
401 increasing temperature. This strong negative trend arises because the fitted R_{day} values decline
402 with leaf temperature (Fig. 6b), rather than increasing in line with V_{cmax} as we assumed. Figure
403 6b indicates that fitted R_{day} values commonly hit the lower bound of zero above 25°C . As R_{day}
404 is estimated as the value of A where $C_i = I^*$, this may indicate that the values of I^* used are
405 inappropriate for these datasets.

406

407 *Sensitivity to temperature dependencies of K_c , K_o and I^**

408 We repeated the exercise of comparing \hat{V}_{cmax} and V_{cmax} using two alternative temperature
409 dependencies of K_c , K_o and I^* for the case where R_{day} was estimated (Fig. 7; Figs S4-5). The
410 accuracy of estimated values was largely insensitive to our three tested assumptions. \hat{V}_{cmax}
411 values estimated with the C13 parameterisation had the lowest RMSE values (average across
412 all PFTs $13.85 \mu\text{mol m}^{-2} \text{s}^{-1}$) and those estimated with BC77 had the largest (average across all
413 PFTs $15.42 \mu\text{mol m}^{-2} \text{s}^{-1}$). However, grouping by PFTs, the mean absolute difference between
414 the different parameterisations was small, *c.* $2 \mu\text{mol m}^{-2} \text{s}^{-1}$. It is also notable that using the
415 BC77 parameterisation resulted in greater errors for herbaceous species, RMSE = *c.* 19 vs. *c.*
416 11 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for B01 and C13 parameterisations. Figures S4-S5 demonstrate that the
417 assumption of a fixed ratio of 0.015 for $R_{\text{day}}:V_{\text{cmax}}$ is still relatively poor for BC77 and C13

418 parameterisations, particularly at low leaf temperatures; the approximation is marginally better
419 for the C13 parameterisation, explaining the lower RMSE values obtained with this
420 parameterisation.

421

422

423

424

425

426

427

428

429

430

431

432

433

434

435

436

437

438

439

440

441

442 **Discussion**

443 In this study we have examined an alternative approach to traditional $A-C_i$ curve analysis for
444 estimating V_{cmax} , an approach that holds promise for greatly expanding the set of species
445 represented in global V_{cmax} datasets. One of the principal concerns about the use of this
446 approach has been that typical measurements of A_{sat} may be limited by RuBP-regeneration
447 rates, rather than Rubisco activity, and hence would yield underestimates of V_{cmax} , especially
448 in wet or warm conditions. Here we have demonstrated that, for photosynthesis measurements
449 taken at ambient CO_2 and under saturating irradiance conditions, values are normally Rubisco-
450 limited and as such, \hat{V}_{cmax} values are in good agreement with V_{cmax} determined from $A-C_i$
451 curves. Residual analysis when using a known R_{day} did not show any bias in V_{cmax} estimation
452 with environmental conditions such as mean annual temperature or precipitation. As a result,
453 our results suggested that the one-point method is likely to be a robust means to resolve V_{cmax}
454 from light-saturated photosynthesis.

455

456 That said, our analysis did identify other, non-trivial sources of error in using the one-point
457 approach. First, we found support for our hypothesis that increased errors would occur at low
458 g_s due to a lower signal-to-noise ratio (hypothesis ii), suggesting that rates of A_{sat} that are not
459 subject to severe stomatal limitation are most suited to this approach. Secondly, poor estimation
460 of the day respiration rate, R_{day} , led to a notable increase in the RMSE of estimates,
461 approximately doubling RMSE from 7.18 to 14.71 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The proportional error in
462 V_{cmax} when estimating R_{day} (i.e. Fig 4b) was on average around 20% for most datasets when
463 grouped by PFT. These errors were larger because we estimated R_{day} using a fixed $R_{\text{day}}:V_{\text{cmax}}$
464 relationship, and this relationship did not capture variation in values of fitted R_{day} . There was
465 strong bias at low and high temperatures, leading to a clear pattern in residuals. In addition,
466 there was higher estimation error ($V_{\text{cmax}} - \hat{V}_{\text{cmax}}$ residuals) at higher V_{cmax} , higher leaf
467 temperatures or at hotter sites (though it should be noted V_{cmax} is typically greater at higher
468 temperatures), and at either very high or very low R_{day} . Having identified and quantified these
469 apparently systematic biases it would of course then be up to individual researchers using this
470 method to decide for themselves what magnitude of error (or bias) was acceptable for the
471 purpose at hand.

472

473 R_{day} is as yet not well understood in terms of responses to environmental variation or
474 temperature dependence and hence is difficult to model (Tcherkez *et al.*, 2012; Heskell *et al.*,
475 2013; Way & Yamori 2014). It is widely understood that estimates of R_{day} obtained from $A-C_i$
476 curves are inaccurate. One reason for the inaccuracy is that the values are extrapolated from
477 small fluxes at low C_i conditions, and hence are subject to noise and possibly gasket-leak
478 effects (Bruhn *et al.* 2002; Hurry *et al.* 2005). In this study we also show that there is a
479 systematic bias in R_{day} estimates with temperature (Figs. 5 and 6), which leads to bias in
480 estimates of \hat{V}_{cmax} . This bias could be potentially due to a number of factors. Firstly, fluxes are
481 lower at lower temperature, so errors due to noise may be greater. Secondly, it is likely that our
482 assumptions for the temperature dependence of either, or both, R_{day} and I^* are incorrect. Fitted
483 estimates of R_{day} showed either no temperature dependence, or a negative temperature
484 dependence, depending on what I^* was assumed (Figs 6, S4 and S5). In contrast, most studies
485 of R_{day} suggest a positive temperature dependence, as is assumed in most TBMs (KC – refs?).
486 The issue may lie with I^* : the most widely-used parameterisation for I^* (B01) resulted in
487 fitted values of R_{day} going to zero at higher temperatures, suggesting this parameterisation may
488 in fact be too temperature-sensitive for many species. This issue also affects photosynthesis
489 values estimated by TBMs using estimates of V_{cmax} obtained from $A-C_i$ curves, because such
490 models commonly use a fixed ratio for $R_{\text{day}}:V_{\text{cmax}}$. The estimates of V_{cmax} are dependent on the
491 fitted values of R_{day} (i.e. our known R_{day}). If models estimate photosynthesis with fitted V_{cmax}
492 but a fixed $R_{\text{day}}:V_{\text{cmax}}$ ratio, the resulting estimates of photosynthesis will be in error.
493 Addressing this problem requires that we develop better empirical parameterisations of the
494 temperature dependences of both I^* and R_{day} , which are applicable across species and climates,
495 rather than the single-species, single-site relationships currently used.

496

497 An alternative approach to using a fixed $R_{\text{day}}:V_{\text{cmax}}$ ratio would be to base estimates of R_{day} on
498 measured values of dark respiration rate, R_{dark} . For example, it could be assumed that $R_{\text{day}} =$
499 $0.6 \times R_{\text{dark}}$ (Kirschbaum and Farquhar 1984) or, alternatively, one might simply set $R_{\text{day}} = R_{\text{dark}}$,
500 as was done by Atkin *et al.*, (2015) when employing the one-point method. However, we note
501 that such approaches would still result in errors when estimating \hat{V}_{cmax} because they both
502 assume a similar temperature dependence for R_{day} and R_{dark} , whereas the fitted temperature

Commented [MD3]: REFs – Kristine? Owen?

503 dependence of R_{day} does not resemble the exponential response typically found for R_{dark} (Figs
504 6, S4 and S5).

505

506 *New research avenues*

507 Despite the error introduced by inaccuracies in R_{day} , the one-point method nevertheless has the
508 potential to provide new insight into variability of V_{cmax} across and within species, PFTs and
509 in relation to other plant traits. Due to logistical constraints, studies measuring V_{cmax} using $A-$
510 C_i curves typically focus on a relatively small number of species, and are biased towards both
511 controlled environments and temperate regions (e.g. Wullschleger 1993; Kattge *et al.*, 2009;
512 Sun *et al.*, 2014; Walker *et al.*, 2014). The results of this paper suggest that measurements of
513 A_{sat} , which are more readily made on a wide range of species under field conditions, can also
514 be used to estimate V_{cmax} using the one-point method. An expanded global V_{cmax} database would
515 greatly facilitate testing of ecophysiological theories of plant trait distribution based on
516 environmentally driven traits (Verheijen *et al.*, 2013, Reich, 2014, van Bodegom *et al.*, 2014),
517 trait-trade offs (Wright *et al.*, 2010, Reu *et al.*, 2011) and optimality concepts (Xu *et al.*, 2012;
518 Prentice *et al.*, 2014; Wang *et al.*, 2014; Ali *et al.*, 2015b). Larger datasets for V_{cmax} would also
519 allow insights into the true scaling of photosynthetic capacity with leaf structural and chemical
520 traits, with the caveat that we have identified some systematic biases in the approach,
521 suggesting it would be best to constrain analysis to data $< 30^\circ\text{C}$ (Fig 5b).

522

523 From a modelling perspective, additional data would serve to improve the underlying evidence
524 base used to constrain model simulations of photosynthesis. For example, Bonan *et al.*, (2011)
525 found that uncertainty due to V_{cmax} was equivalent to uncertainties due to structural errors (e.g.
526 scaling photosynthesis and stomatal conductance from the leaf to the canopy), accounting for
527 a $\sim 30 \text{ Pg C year}^{-1}$ variation in modelled gross primary productivity in CLM4. A number of
528 models (e.g. CABLE, JULES, CLM4) assume that the J_{max} parameter and/or the autotrophic
529 respiration are proportional to V_{cmax} . Therefore, this single parameter has a marked impact on
530 modelled carbon flux and improvements in the V_{cmax} parameter have the potential to constrain
531 multiple facets of current TBMs. For example, Dietze *et al.*, (2014a) showed that inclusion of
532 even small observational datasets of V_{cmax} could adequately constrain the parameterisation of
533 the Ecosystem Demography (ED2) model across a range of biomes. Furthermore, it is now

534 commonplace in some modelling studies to simulate vegetation fluxes considering the full
535 uncertainty of key parameters, rather than assuming a PFT can be described by a single value
536 (Ziehn *et al.*, 2011; Wang *et al.*, 2012).

537

538 It should be noted that our analysis calls into question the modelling assumption that J_{\max} is
539 proportional to V_{cmax} , as shown by the high variability in C_i transition points observed across
540 our data set (Figure 2). These transition points can be used to estimate the ratio of $J_{\max} / V_{\text{cmax}}$.
541 We estimated this ratio at 25°C from the transition points, and found a mean value of 1.9 with
542 a large inter-quartile range, stretching from 1.68 to 2.14. As noted above, there was some
543 difference in the median transition point (and hence $J_{\max} / V_{\text{cmax}}$ ratio) among PFTs, but the
544 variability within a PFT is considerably larger than between PFTs. While the one-point method
545 can provide insights into variation in V_{cmax} , it does not enable us to develop better
546 parameterisations for other key photosynthetic parameters. There remains a need for full $A-C_i$
547 curves to also quantify the variability in $J_{\max} / V_{\text{cmax}}$ ratio, or as an alternative, cluster sampling
548 approaches (e.g. extensively sampling of the photosynthesis-light response curve) as proposed
549 by Dietze (2014b).

550

551 There is also the potential for a complementary set of parameter estimates to be obtained
552 through a re-examination of existing A_{sat} datasets. Large quantities of field-measured A_{sat} data
553 currently exist in global databases, for example ~1500 species in Maire *et al.*, (2015) and 2192
554 species in TRY (Kattge *et al.*, 2011). By putting together V_{cmax} data derived from $A-C_i$ curves
555 with V_{cmax} values determined from the one-point method (i.e., \hat{V}_{cmax}), there is potential to
556 generate a database consisting of data for thousands of species, for many hundred sites around
557 the world. Consistent conversion of A_{sat} to V_{cmax} values in worldwide datasets would be strongly
558 beneficial, enabling a wider characterisation of V_{cmax} variations across the globe, and better
559 quantification of relationships between V_{cmax} and other leaf traits (Walker *et al.*, 2014) and with
560 site climate (Ali *et al.*, 2015). However, it is important to note that application of the one-point
561 method to these datasets may involve additional sources of error. For example, Kattge *et al.*
562 (2009) estimated \hat{V}_{cmax} using a one-point method applied to A_{sat} data that did not include
563 complementary values of C_i , and thus estimated C_i as a constant fraction (0.8) of C_a . In our
564 dataset, the 25th and 75th quartiles for the $C_i:C_a$ ratio were 0.60 – 0.75; use of a constant value

565 would thus have introduced considerable additional error. Application of the one-point method
566 to species-mean values of A_{sat} and g_s , such as those collated by Maire *et al.* (2015), would also
567 be subject to systematic error from averaging a non-linear function. Thus, application of the
568 one-point method in these circumstances needs to be done with caution.

569

570 This manuscript presents an empirical justification for using the one-point method, which we
571 conclude can be used to estimate accurate values of V_{cmax} , for an estimate that we labelled \hat{V}_{cmax}
572 for distinction from intensively measured curves. We stress that continued measurement of
573 plant behaviour using detailed $A-C_i$ response curves is still invaluable and, indeed, “best-
574 practice”. Fitting the model of Farquhar *et al.*, (1980) to data has provided a tried and tested
575 way to evaluate and interpret plant physiological behaviour in the field and lab alike. The one-
576 point method tested here *complements* the traditional approach, potentially allowing us to
577 greatly expand plant trait datasets of maximum carboxylation efficiency.

578

579

580

581

582

583

584

585

586

587

588

589

590

591

592

593

594 **Acknowledgements**

595 MDK was supported by the Australian Research Council (ARC) Linkage grant (LP140100232).
596 Y-SL was jointly supported by ARC funding to ICP and IJW (DP120103600) and by TERN
597 eMAST (Ecosystem Modelling and Scaling Infrastructure). We also acknowledge ARC
598 support to DE, BEM, IJW and OA (DP0986823, DP110105102, DP130101252, CE140100008
599 and FT0991448). DSE and KYC gratefully acknowledge the Birmingham Institute of Forest
600 Research, the Institute of Advanced Studies at the University of Birmingham, and the Western
601 Sydney University for support during manuscript preparation. ICP is the AXA Research Fund
602 Chair in Biosphere and Climate Impacts and his part in this research contributes to the Chair
603 programme and to the Imperial College initiative ‘Grand Challenges in Ecosystems and the
604 Environment’. AR was supported by the Next-Generation Ecosystem Experiments (NGEE
605 Arctic) project that is supported by the Office of Biological and Environmental Research in the
606 Department of Energy, Office of Science. AR and SPS were also supported through the United
607 States Department of Energy contract No. DE-SC00112704 to Brookhaven National
608 Laboratory. HFT is supported by an international Macquarie University International Research
609 Scholarship (iMQRES) and HFT and BE are supported by TERN eMAST. The Terrestrial
610 Ecosystem Research Network (TERN) is supported by the Australian Government through the
611 National Collaborative Research Infrastructure Strategy (NCRIS). PM Support acknowledged
612 from: ARC FT110100457 and NERC NE/J011002/1. Finally we acknowledge support in part
613 to the NSF grant 1146206 and the Moore Foundation grant 3001 to G.P. Asner and to data
614 collected as part of RAINFOR to O. Philips.

615

616 All data analysis and plots were written in Python; in particular we made use of the Scipy
617 (Jones *et al.*, 2001), LMFIT (Neville *et al.* 2014) and Matplotlib libraries (Hunter, 2007).

618

619

621 **Figure Captions**

622 Figure 1: Conceptual figure demonstrating how errors could arise when estimating V_{cmax} using
623 the one-point method. When R_{day} is correct (dark yellow point) and A_{sat} is Rubisco limited
624 (black point) V_{cmax} is correctly estimated (dashed purple line). When A_{sat} is RuBP-regeneration
625 limited (blue point) V_{cmax} will be under-estimated (dashed blue line). If R_{day} is over-estimated
626 (green point) V_{cmax} will be over-estimated (dashed green line).

627

628 Figure 2: Relationship between ambient C_i and the C_i value at the transition point obtained
629 from $A-C_i$ curve fitting. In panel (a) data shown are for individual species, but have been
630 grouped (coloured) by plant functional type: EBF - evergreen broadleaved forest, DBF -
631 deciduous broadleaved forest, ENF - evergreen needle leaved forest, DNF - deciduous needle
632 leaved forest, DSB - deciduous shrubs and HRB - herbaceous species. The data have also been
633 binned (bin size = 10), with the original data shown in a matching semi-transparent colour. In
634 panel (b) the box and whisker plots show the C_i value at the transition point (line, median, box,
635 inter-quartile range), with bars extending to 1.5 times the inter-quartile range. Dots outside of
636 the box and whiskers show outlying points.

637

638 Figure 3: Comparison between V_{cmax} values estimated from traditional $A-C_i$ curve fitting and
639 V_{cmax} estimated from one-point method, \hat{V}_{cmax} . Panel (a) and (b) show the effect of using a
640 known and an estimated R_{day} (1.5% of V_{cmax}), respectively. Data shown are for all 1318 species
641 but have been coloured as in Figure 2 to match representative plant functional types. Regression
642 lines have been fit to the raw data (1318 species measurements) and coloured to match plant
643 functional types.

644

645 Figure 4: Residuals ($V_{\text{cmax}} - \hat{V}_{\text{cmax}}$) shown as a function of V_{cmax} , ambient g_s , estimated R_{day} and
646 C_i . Data were binned (panels (a) and (b) bin size = 10; panel (c) and (d) bin size = 0.05; panels
647 (e) and (f) bin size = 0.25), panels (e) and (f), bin size = 10), with the original data shown in a
648 matching semi-transparent colour. Data shown are for all 1318 species but have been coloured
649 as in Figure 2 to match representative plant functional types. A significant ($p < 0.05$) trend in
650 the residuals is shown by a solid black line. Trend lines have been fit to the raw data (1318

651 species measurements). In panels (a) and (b) the grey dashed lines represent 5 (dot-dash) and
652 10% (dot-dot) error, respectively.

653

654 Figure 5: Residuals ($V_{\text{cmax}} - \hat{V}_{\text{cmax}}$) shown as a function of leaf temperature, mean annual
655 temperature and mean annual precipitation. Data in the residual panels have been binned
656 (panels (a), (b), (c) and (d) bin size = 0.5; panels (e) and (f), bin size = 100), with the original
657 data shown in a matching semi-transparent colour. Data shown are for all 1318 species, but
658 have been coloured as in Figure 2 to match representative plant functional types. A significant
659 ($p < 0.05$) trend in the residuals is shown by a solid black line. Trend lines have been fit to the
660 raw data (1318 species measurements).

661

662 Figure 6: Fitted $R_{\text{day}}:V_{\text{cmax}}$ ratio (a) and (b) R_{day} as a function of leaf temperature using the
663 Bernacchi *et al.* (2001) parameters. Data shown are for all 1318 species, but have been coloured
664 as in Figure 2 to match representative plant functional types. The horizontal red line shows the
665 $R_{\text{day}}:V_{\text{cmax}}$ commonly assumed by terrestrial biosphere models following Collatz *et al.* (1991).

666

667 Figure 7: Relationship between V_{cmax} values estimated from the traditional approach and \hat{V}_{cmax}
668 values using three different sets of K_c , K_o , and I^* parameters. Data shown are for all 1318
669 species, but have been coloured as in figure 2 to match representative plant functional types.
670 Regression lines have been fit to the raw data (1318 species measurements) and coloured to
671 match plant functional types.

672

673 Supplementary Figure 1: Climatic space covered by this study shown by density hexagons.
674 Over-plotted colour symbols represent sampled species, grouped by plant functional type.

675

676 Supplementary Figure 2: Residuals ($V_{\text{cmax}} - \hat{V}_{\text{cmax}}$) shown as a function of a moisture index and
677 elevation. Data in the residual panels have been binned ((panels (a) and (b) bin size = 0.1;
678 panels (c) and (d), bin size = 100), with the original data shown in a matching semi-transparent

679 colour. Data shown are for all 1318 species, but have been coloured as in figure 2 to match
680 representative plant functional types. A significant ($p < 0.05$) trend in the residuals is shown by
681 a solid black line. Trend lines have been fit to the raw data (1318 species measurements).

682

683 Supplementary Figure 3: Residuals $V_{\text{cmax}} - \hat{V}_{\text{cmax}}$ shown as a function of the number annual
684 growing degree days above $> 0^\circ\text{C}$ and $> 5^\circ\text{C}$, Data in the residual panels have been binned
685 (panels (a), (b), (c) and (d) bin size = 0.5), with the original data shown in a matching semi-
686 transparent colour. Data shown are for all 1318 species, but have been coloured as in figure 2
687 to match representative plant functional types. Significant ($p < 0.05$) trends in absolute and non-
688 absolute residuals are shown by the solid red and black lines, respectively. These trends lines
689 have been fit to the raw data (1318 species measurements).

690

691 Supplementary Figure 4: Fitted $R_{\text{day}}:V_{\text{cmax}}$ ratio (a) and (b) R_{day} as a function of leaf temperature
692 using the Badger & Collatz (1977) parameters. Data shown are for all 1318 species, but have
693 been coloured as in figure 2 to match representative plant functional types. The horizontal red
694 line shows the $R_{\text{day}}:V_{\text{cmax}}$ commonly assumed by terrestrial biosphere models following Collatz
695 *et al.* (1991).

696

697 Supplementary Figure 5: Fitted $R_{\text{day}}:V_{\text{cmax}}$ ratio (a) and (b) R_{day} as a function of leaf temperature
698 using the Crous *et al.* (2013) parameters. Data shown are for all 1318 species, but have been
699 coloured as in figure 2 to match representative plant functional types. The horizontal red line
700 shows the $R_{\text{day}}:V_{\text{cmax}}$ commonly assumed by terrestrial biosphere models following Collatz *et*
701 *al.* (1991).

702

703

704

705 **References**

706 **Ali AA, Xu C, Rogers A, McDowell NG, Medlyn BE, Fisher RA, Wullschleger SD, Reich**
707 **PB, Vrugt JA, Bauerle WL et al. 2015a.** Global scale environmental control of plant
708 photosynthetic capacity. *Ecological Applications*, in press.

709 **Ali AA, Xu C, Rogers A, Fisher RA, Wullschleger SD, McDowell NG, Massoud EC, Vrugt**
710 **JA, Muss JD, Fisher JB et al. 2015b.** A global scale mechanistic model of the photosynthetic
711 capacity. *Geoscientific Model Development Discussions* 8: 6217–6266.

712 **Anderson L, Malhi Y, Ladle R, Aragao L, Shimabukuro Y, Phillips O, Baker T, Costa A,**
713 **Espejo J, Higuchi N et al. 2009.** Influence of landscape heterogeneity on spatial patterns of
714 wood productivity, wood specific density and above ground biomass in Amazonia.
715 *Biogeosciences* 6: 1883–1902.

716 **Atkin OK, Bloomfield KJ, Reich PB, Tjoelker MG, Asner GP, Bonal D, Bönisch G,**
717 **Bradford M, Cernusak LA, Cosio EG et al. 2015.** Global variability in leaf respiration in
718 relation to climate, plant functional types and leaf traits. *New Phytologist* 206: 614–636.

719 **Badger MR and Collatz GJ. 1977** Studies on the kinetic mechanism of RuBP carboxylase
720 and oxygenase reactions, with particular reference to the effect of temperature on kinetic
721 parameters. *Carnegie Inst Wash Yearbook*, 76: 355–361.

722 **Bernacchi C, Singsaas E, Pimentel C, Portis Jr A, Long S. 2001.** Improved temperature
723 response functions for models of Rubisco-limited photosynthesis. *Plant, Cell & Environment*
724 24: 253–259.

725 **Bonan GB, Lawrence PJ, Oleson KW, Levis S, Jung M, Reichstein M, Lawrence DM,**
726 **Swenson SC. 2011.** Improving canopy processes in the Community Land Model version 4
727 (CLM4) using global flux fields empirically inferred from FLUXNET data. *Journal of*
728 *Geophysical Research* 116: G02014.

729 **Brooks A, Farquhar G. 1985.** Effect of temperature on the CO₂/O₂ specificity of ribulose-1,
730 5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. *Planta* 165: 397–
731 406.

732 **Bruhn D, Mikkelsen TN, Atkin OK. 2002.** Does the direct effect of atmospheric CO₂
733 concentration on leaf respiration vary with temperature? Responses in two species of *Plantago*
734 that differ in relative growth rate. *Physiologia Plantarum*, 114: 57-64.

735 **Chen J-L, Reynolds JF, Harley PC, Tenhunen JD. 1993.** Coordination theory of leaf
736 nitrogen distribution in a canopy. *Oecologia* 93: 63–69.

737 **Clark DB, Mercado LM, Sitch S, Jones CD, Gedney N, Best MJ, Pryor M, Rooney GG,**
738 **Essery RLH, Blyth E, et al. 2011.** The Joint UK Land Environment Simulator (JULES), model
739 description - Part 2: Carbon fluxes and vegetation dynamics. *Geoscientific Model Development*
740 4: 701–722.

741 **Crous KY, Quentin AG, Lin Y-S, Medlyn BE, Williams DG, Barton CV, Ellsworth DS.**
742 **2013.** Photosynthesis of temperate *Eucalyptus globulus* trees outside their native range has
743 limited adjustment to elevated CO₂ and climate warming. *Global Change Biology* 19: 3790–
744 3807.

745 **Crous KY, Zaragoza-Castells J, Ellsworth DS, Duursma RA, Löw M, Tissue DT and**
746 **Atkin OK. 2012.** Light inhibition of leaf respiration in field-grown *Eucalyptus saligna* in
747 whole-tree chambers under elevated atmospheric CO₂ and summer drought. *Plant, Cell and*
748 *Environment* 35(5) : 966-981

749 **De Kauwe MG, Lin, Y-S, Medlyn BE. 2015.** FitFarquharModel: Vcmax one-point method.
750 Zenodo. DOI: 10.5281/zenodo.30954.

751 **del Aguila-Pasquel J, Doughty CE, Metcalfe DB, Silva-Espejo JE, Girardin CA, Chung**
752 **Gutierrez JA, Navarro-Aguilar GE, Quesada CA, Hidalgo CG, Reyna Huaymacari JM**
753 **et al. 2014.** The seasonal cycle of productivity, metabolism and carbon dynamics in a wet
754 aseasonal forest in north-west Amazonia (Iquitos, Peru). *Plant Ecology & Diversity* 7: 71–83.

755 **Dietze, MC, Serbin SP, Davidson C, Desai AR, Feng X, Kelly R, Kooper R, LeBauer D,**
756 **Mantooth J, McHenry K, Wang D 2014a.** A quantitative assessment of a terrestrial biosphere
757 model's data needs across North American biomes. *Journal of Geophysical Research-*
758 *Biogeosciences*, 119: 286-300.

773 **Dietze M. 2014b.** Gaps in knowledge and data driving uncertainty in models of photosynthesis.
774 *Photosynthesis Research*, 119:3–14.

775 **Domingues TF, Yoko Ishida F, Feldpausch TR, Grace J, Meir P, Saiz G, Sene O et al.**
776 **2015.** Biome-specific effects of nitrogen and phosphorus on the photosynthetic characteristics
777 of trees at a forest-savanna boundary in Cameroon. *Oecologia* 178, 659-672.

778 **Domingues TF, Berry JA, Martinelli LA, Ometto JP, Ehleringer JR. 2005.**
779 Parameterization of canopy structure and leaf-level gas exchange for an eastern Amazonian
780 tropical rain forest (Tapajos National Forest, Para, Brazil). *Earth Interactions* 9: 1–23.

781 **Domingues TF, Meir P, Feldpausch TR, Saiz G, Veenendaal EM, Schrodt F, Bird M,**
782 **Djagbletey G, Hien F, Compaore H et al. 2010.** Co-limitation of photosynthetic capacity by
783 nitrogen and phosphorus in West Africa woodlands. *Plant, Cell & Environment* 33: 959–980.

784 **Dreyer, E, Le Roux X, Montpied P, Daudet FA, Masson, Frederic. 2001.** Temperature
785 response of leaf photosynthetic capacity in seedlings from seven temperate tree species. *Tree*
786 *Physiology*, 21, 223-232.

787 **Dubois JJB, Fiscus EL, Booker FL, Flowers MD, Reid CD. 2007.** Optimizing the statistical
788 estimation of the parameters of the Farquhar–von Caemmerer–Berry model of photosynthesis.
789 *New Phytologist* 176: 402–414.

790 **Ellsworth DS, Crous KY, Lambers H, Cooke J. 2015.** Phosphorus recycling in
791 photorespiration maintains high photosynthetic capacity in woody species. *Plant, Cell &*
792 *Environment* 38: 1142–1156.

793 **Ellsworth DS, Reich PB, Naumburg ES, Koch GW, Kubiske ME, Smith SD. 2004.**
794 Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO₂
795 across four free-air CO₂ enrichment experiments in forest, grassland and desert. *Global Change*
796 *Biology* 10: 2121–2138.

797 **Ellsworth DS, Thomas R, Crous KY, Palmroth S, Ward E, Maier C, DeLucia E, Oren R.**
798 **2012.** Elevated CO₂ affects photosynthetic responses in canopy pine and subcanopy deciduous
799 trees over 10 years: a synthesis from Duke FACE. *Global Change Biology* 18: 223–242.

800 **Evans, J. 1986.** The relationship between carbon-dioxide-limited photosynthetic rate and
801 ribulose-1,5-bisphosphate-carboxylase content in two nuclear-cytoplasm substitution lines of
802 wheat, and the coordination of ribulose-bisphosphate-carboxylation and electron-transport
803 capacities. *Planta*, 167:351-358.

804 **Farquhar G, von Caemmerer S, Berry J. 1980.** A biochemical model of photosynthetic CO₂
805 assimilation in leaves of C₃ species. *Planta* 149: 78–90.

806 **Feng X, Dietze M. 2013.** Scale dependence in the effects of leaf ecophysiological traits on
807 photosynthesis: Bayesian parameterization of photosynthesis models. *New Phytologist* 200:
808 1132–1144.

809 **Field CB, Mooney HA. 1986.** The Economy of Plant Form and Function. In: Givnish TJ, ed.
810 Cambridge University Press, 22–55.

811 **Flexas J, Ortuño M, Ribas-Carbo M, Diaz-Espejo A, Flórez-Sarasa I, Medrano H. 2007.**
812 Mesophyll conductance to CO₂ in *Arabidopsis thaliana*. *New Phytologist* 175: 501–511.

813 **Friedlingstein P, Meinshausen M, Arora VK, Jones CD, Anav A, Liddicoat SK, Knutti R.**
814 **2014.** Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *Journal of*
815 *Climate* 27: 511–526.

816 **Gallego-Sala A, Clark JM, House JI, Orr HG, Prentice IC, Smith P, Farewell T,**
817 **Chapman SJ. 2010.** Bioclimatic envelope model of climate change impacts on blanket
818 peatland distribution in Great Britain. *Climate Research*, 45, 151–162.

819 **Girardin CA, Espejob JES, Doughty CE, Huasco WH, Metcalfe DB, Durand-Baca L,**
820 **Marthews TR, Aragao LE, Farfán-Rios W, García-Cabrera K et al. 2014a.** Productivity
821 and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecology*
822 *& Diversity* 7: 107–123.

823 **Girardin C, Malhi Y, Feeley K, Rapp J, Silman M, Meir P, Huaraca Huasco W, Salinas**
824 **N, Mamani M, Silva-Espejo J et al. 2014b.** Seasonality of above-ground net primary
825 productivity along an Andean altitudinal transect in Peru. *Journal of Tropical Ecology* 30: 503–
826 519.

827 **Grassi G, Vicinelli E, Ponti F, Cantoni L, Magnani F. 2005.** Seasonal and interannual
828 variability of photosynthetic capacity in relation to leaf nitrogen in a deciduous forest plantation
829 in northern Italy. *Tree Physiology* 25: 349–360.

830 **Gu F, Zhang Y, Tao B, Wang Q, Yu G, Zhang L, Li K. 2010.** Modeling the effects of
831 nitrogen deposition on carbon budget in two temperate forests. *Ecological Complexity* 7: 139–
832 148.

833 **Heskel MA, Atkin OK, Turnbull MH, Griffin KL. 2013.** Bringing the Kok effect to light: a
834 review on the integration of daytime respiration and net ecosystem exchange. *Ecosphere* 4:
835 art98.

836 **Hirose T, Werger M. 1987.** Maximizing daily canopy photosynthesis with respect to the leaf
837 nitrogen allocation pattern in the canopy. *Oecologia* 72: 520–526.

838 **Huasco WH, Girardin CA, Doughty CE, Metcalfe DB, Baca LD, Silva-Espejo JE,**
839 **Cabrera DG, Aragão LE, Davila AR, Marthews TR et al. 2014.** Seasonal production,
840 allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the
841 Peruvian Andes. *Plant Ecology & Diversity* 7: 125–142.

842 **Hurry V, Igamberdiev AU, Keerberg O, Pärnik T, Atkin OK, Zaragoza-Castells J,**
843 **Gardeström P. 2005.** Respiration in photosynthetic cells: gas exchange components,
844 interactions with photorespiration and the operation of mitochondria in the light. In H. Lambers
845 and M. Ribas-Carbo (eds.) *Plant Respiration: From Cell to Ecosystem*. pp 43–61. Springer,
846 The Netherlands.

847 **Jordan DB, Ogren WL. 1984.** The CO₂/O₂ specificity of ribulose 1,5-bisphosphate
848 carboxylase/oxygenase. *Planta* 161: 308–313.

849 **Kattge J, Diaz S, Lavorel S, Prentice I, Leadley P, Bönisch G, Garnier E, Westoby M,**
850 **Reich PB, Wright I et al. 2011.** TRY—a global database of plant traits. *Global Change Biology*
851 17: 2905–2935.

852 **Kattge J, Knorr W. 2007.** Temperature acclimation in a biochemical model of photosynthesis:
853 a reanalysis of data from 36 species. *Plant, Cell & Environment* 30: 1176–1190.

854 **Kattge J, Knorr W, Raddatz T, Wirth C. 2009.** Quantifying photosynthetic capacity and its
855 relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global*
856 *Change Biology* 15: 976–991.

857 **Kirschbaum, MU, Farquhar, GD. 1984.** Temperature Dependence of Whole-leaf
858 Photosynthesis in *Eucalyptus pauciflora* Sieb. Ex Spreng. *Australian Journal of Plant*
859 *Physiology*, 11: 519-538.

860 **Kosugi Y, Shibata S, Kobashi S. 2003.** Parameterization of the CO₂ and H₂O gas exchange
861 of several temperate deciduous broad-leaved trees at the leaf scale considering seasonal
862 changes. *Plant, Cell & Environment* 26: 285–301.

863 **Kowalczyk EA, Wang YP, Wang P, Law RH, Davies HL. 2006.** *The CSIRO Atmosphere*
864 *Biosphere Land Exchange (CABLE) model for use in climate models and as an offline model.*
865 CSIRO.

866 **Leuning R. 1997.** Scaling to a common temperature improves the correlation between the
867 photosynthesis parameters J_{max} and V_{cmax}. *Journal of Experimental Botany* 48: 345–347.

868 **Levenberg K. 1944.** A method for the solution of certain non-linear problems in least squares.
869 *Quarterly Journal of Applied Mathematics* 2: 164–168.

870 **Lin Y-S, Medlyn BE, De Kauwe MG, Ellsworth DS. 2013.** Biochemical photosynthetic
871 responses to temperature: how do interspecific differences compare with seasonal shifts? *Tree*
872 *physiology* 33: 793–806.

873 **Long S, Bernacchi C. 2003.** Gas exchange measurements, what can they tell us about the
874 underlying limitations to photosynthesis? Procedures and sources of error. *Journal of*
875 *Experimental Botany* 54: 2393–2401.

876 **Maire V, Martre P, Kattge J, Gastal F, Esser G, Fontaine S, Soussana J-F. 2012.** The
877 coordination of leaf photosynthesis links C and N fluxes in C3 plant species. *PLoS one* 7:
878 e38345.

879 **Maire V, Wright IJ, Prentice IC, Batjes NH, Bhaskar R, Bodegom PM, Cornwell WK,**
880 **Ellsworth D, Niinemets Ü, Ordóñez A et al. 2015.** Global effects of soil and climate on leaf
881 photosynthetic traits and rates. *Global Ecology and Biogeography* 24: 706–717.

882 **Malhi Y, Silman M, Salinas N, Bush M, Meir P, Saatchi S. 2010.** Introduction: elevation
883 gradients in the tropics: laboratories for ecosystem ecology and global change research. *Global*
884 *Change Biology* 16: 3171–3175.

885 **Malhi Y, Farfán Amézquita F, Doughty CE, Silva-Espejo JE, Girardin CA, Metcalfe DB,**
886 **Aragão LE, Huaraca-Quispe LP, Alzamora-Taype I, Eguiluz-Mora L et al. 2014.** The
887 productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western
888 Amazonia, Peru. *Plant Ecology & Diversity* 7: 85–105.

889 **Marquardt DW. 1963.** An algorithm for least-squares estimation of nonlinear parameters.
890 *Journal of the Society for Industrial & Applied Mathematics* 11: 431–441.

891 **Medlyn BE, Loustau D, Delzon S. 2002a.** Temperature response of parameters of a
892 biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine
893 (*Pinus pinaster* Ait.). *Plant Cell and Environment* 25: 1155–1165.

894 **Medlyn B, Dreyer E, Ellsworth D, Forstreuter M, Harley P, Kirschbaum M, Le Roux X,**
895 **Montpied P, Strassmeyer J, Walcroft A et al. 2002b.** Temperature response of parameters
896 of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant*
897 *Cell and Environment* 25: 1167–1179.

898 **Meir P, Kruijt B, Broadmeadow M, Barbosa E, Kull O, Carswell F, Nobre A, Jarvis P.**
899 **2002.** Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf
900 nitrogen concentration and leaf mass per unit area. *Plant, Cell & Environment* 25: 343–357.

901 **Miao Z, Xu M, Lathrop RG, Wang Y. 2009.** Comparison of the A–Cc curve fitting methods
902 in determining maximum ribulose 1·5-bisphosphate carboxylase/oxygenase carboxylation rate,
903 potential light saturated electron transport rate and leaf dark respiration. *Plant, Cell &*
904 *Environment* 32: 109–122.

905 **New M, Hulme M, Jones P. 1999.** Representing twentieth-century space–time climate
906 variability. Part I: Development of a 1961–90 mean monthly terrestrial climatology. *Journal of*
907 *Climate*, 12, 829–856.

908 **Newville M, Stensitzki T, Allen DB, Ingargiola A. 2014.** LMFIT: Non-Linear Least-Square
909 Minimization and Curve-Fitting for Python. Zenodo. Doi: 10.5281/zenodo.11813.

910 **Niinemets Ü. 1998.** Adjustment of foliage structure and function to a canopy light gradient in
911 two co-existing deciduous trees. Variability in leaf inclination angles in relation to petiole
912 morphology. *Trees* 12: 446–451.

913 **Niinemets Ü. 1999.** Research review. Components of leaf dry mass per area–thickness and
914 density–alter leaf photosynthetic capacity in reverse directions in woody plants. *New*
915 *Phytologist* 144: 35–47.

916 **Niinemets Ü. 2014.** Is there a species spectrum within the world-wide leaf economics spectrum?
917 Major variations in leaf functional traits in the Mediterranean sclerophyll *Quercus ilex*. *New*
918 *Phytologist*, 205: 79-96.

919 **Niinemets Ü, Ellsworth DS, Lukjanova A, Tobias M. 2001.** Site fertility and the
920 morphological and photosynthetic acclimation of *Pinus sylvestris* needles to light. *Tree*
921 *Physiology* 21: 1231–1244.

922 **Niinemets Ü, Tenhunen J. 1997.** A model separating leaf structural and physiological effects
923 on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. *Plant, Cell*
924 *& Environment* 20: 845–866.

925 **Oleson KW, Lawrence DM, Bonan GB, Drewniak B, Huang M, Koven CD, Levis S, Li F,**
926 **Riley WJ, Subin ZM et al. 2013.** *Technical Description of version 4.5 of the Community Land*
927 *Model (CLM)*. National Center for Atmospheric Research, P.O. Box 3000, Boulder, Colorado.

928 **Ordonez A, Olf H. 2013.** Do alien plant species profit more from high resource supply than
929 natives? A trait-based analysis. *Global Ecology and Biogeography* 22: 648–658.

930 **Patrick LD, Ogle K, Tissue DT. 2009.** A hierarchical Bayesian approach for estimation of
931 photosynthetic parameters of C3 plants. *Plant, Cell & Environment* 32: 1695–1709.

932 **Piao S, Sitch S, Ciais P, Friedlingstein P, Peylin P, Wang X, Ahlström A, Anav A,**
933 **Canadell JG, Cong N et al. 2013.** Evaluation of terrestrial carbon cycle models for their
934 response to climate variability and to CO₂ trends. *Global Change Biology* 19: 2117–2132.

935 **Prentice IC, Dong N, Gleason SM, Maire V, Wright IJ. 2014.** Balancing the costs of carbon
936 gain and water transport: testing a new theoretical framework for plant functional ecology.
937 *Ecology Letters* 17: 82–91.

938 **Prentice IC, Farquhar G, Fasham M, Goulden ML, Heimann M, Jaramillo V, Khashgi**
939 **H, LeQuéré C, Scholes RJ, Wallace DW. 2001.** The Carbon Cycle and Atmospheric Carbon
940 Dioxide In: *Climate Change 2001: the Scientific Basis. Contributions of Working Group I to*
941 *the Third Assessment Report of the Intergovernmental Panel on Climate Change*. In: Houghton
942 JT, Ding Y, Griggs DJ, Noguer M, Linden van der, P.J. DX, Maskell K, Johnson CA, eds.
943 Cambridge University Press, 185–237.

944 **Reich PB, Luo Y, Bradford JB, Poorter H, Perry CH, Oleksyn J. 2014.** Temperature drives
945 global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of the*
946 *National Academy of Sciences* 111: 13721–13726.

947 **Reich PB, Walters MB, Ellsworth DS. 1997.** From tropics to tundra: global convergence in
948 plant functioning. *Proceedings of the National Academy of Sciences* 94: 13730–13734.

949 **Reu B, Zaehle S, Proulx R, Bohn K, Kleidon A, Pavlick R, Schmittlein S. 2011.** The role
950 of plant functional trade-offs for biodiversity changes and biome shifts under scenarios of
951 global climatic change. *Biogeosciences* 8: 1255–1266.

952 **Rogers A. 2014.** The use and misuse of $V_{c,max}$ in Earth System Models. *Photosynthesis*
953 *research* 119: 15–29.

954 **Rogers A, Ellsworth DS, Humphries SW. 2001.** Possible explanation of the disparity
955 between the in vitro and in vivo measurements of Rubisco activity: a study in loblolly pine
956 grown in elevated pCO₂. *Journal of Experimental Botany* 52: 1555–1561.

957 **Rogers A, Humphries SW. 2000.** A mechanistic evaluation of photosynthetic acclimation at
958 elevated CO₂. *Global Change Biology* 6: 1005–1011.

959 **Serbin SP, Singh A, Desai AR, Dubois SG, Jablonski AD, Kingdon CC, Kruger EL and**
960 **Townsend PA. 2015.** Remotely estimating photosynthetic capacity, and its response to
961 temperature, in vegetation canopies using imaging spectroscopy. *Remote Sensing of*
962 *Environment*, 167: 78-87

963 **Sharkey TD. 1985.** Photosynthesis in intact leaves of C3 plants: physics, physiology and rate
964 limitations. *The Botanical Review* 51: 53–105.

965 **Sharkey TD, Bernacchi CJ, Farquhar GD, Singsaas EL. 2007.** Fitting photosynthetic
966 carbon dioxide response curves for C3 leaves. *Plant, Cell & Environment* 30: 1035–1040.

967 **Sun Y, Gu L, Dickinson RE, Pallardy SG, Baker J, Cao Y, DaMatta FM, Dong X,**
968 **Ellsworth D, Van Goethem D et al. 2014.** Asymmetrical effects of mesophyll conductance
969 on fundamental photosynthetic parameters and their relationships estimated from leaf gas
970 exchange measurements. *Plant, Cell & Environment* 37: 978–994.

971 **Tarvainen L, Wallin G, Rantfors M, Uddling J. 2013.** Weak vertical canopy gradients of
972 photosynthetic capacities and stomatal responses in a fertile Norway spruce stand. *Oecologia*
973 173: 1179–1189.

974 **Tcherkez G, Boex-Fontvieille E, Mahé A, Hodges M. 2012.** Respiratory carbon fluxes in
975 leaves. *Current opinion in plant biology* 15: 308–314.

976 **Uddling J, Teclaw RM, Pregitzer KS, Ellsworth DS. 2009.** Leaf and canopy conductance in
977 aspen and aspen-birch forests under free-air enrichment of carbon dioxide and ozone. *Tree*
978 *physiology* 29: 1367–1380.

979 **van Bodegom PM, Douma JC, Verheijen LM. 2014.** A fully traits-based approach to
980 modeling global vegetation distribution. *Proceedings of the National Academy of Sciences* 111:
981 13733–13738.

982 **Verheijen L, Brovkin V, Aerts R, Bönish G, Cornelissen J, Kattge J, Reich P, Wright I,**
983 **Van Bodegom P. 2013.** Impacts of trait variation through observed trait-climate relationships
984 o performance of a representative Earth System Model: a conceptual analysis. *Biogeosciences*
985 10: 5497–5515.

986 **von Caemmerer S, Farquhar GD, Berry JA. 2009** Biochemical model of C3 photosynthesis.
987 In: Laik A, Nedbal L, Govindjee (eds). *Photosynthesis in silico: understanding complexity*
988 from molecules to ecosystems. Springer Science + Business Media B.V., Dordrecht, pp 209–
989 230.

990 **von Caemmerer S. 2000.** *Biochemical models of leaf photosynthesis.* Techniques in Plant
991 Science, No. 2. CSIRO Publishing, Collingwood.

992 **Walker AP, Beckerman AP, Gu L, Kattge J, Cernusak LA, Domingues TF, Scales JC,**
993 **Wohlfahrt G, Wullschlegel SD, Woodward FI. 2014.** The relationship of leaf photosynthetic
994 traits–V_{max} and J_{max}–to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-
995 analysis and modeling study. *Ecology and Evolution*, 4: 3218–3235.

996 **Wang Y, Lu X, Wright I, Dai Y, Rayner P, Reich P. 2012.** Correlations among leaf traits
997 provide a significant constraint on the estimate of global gross primary production.
998 *Geophysical Research Letters* 39: L19405.

999 **Wang H, Prentice I, Davis T. 2014.** Biophysical constraints on gross primary production by
1000 the terrestrial biosphere. *Biogeosciences* 11: 5987–6001.

1001 **Way DA, Yamori W. 2014.** Thermal acclimation of photosynthesis: on the importance of
1002 adjusting our definitions and accounting for thermal acclimation of respiration. *Photosynthesis*
1003 *research* 119: 89–100.

- 1004 **Weerasinghe LK, Creek D, Crous KY, Xiang S, Liddell MJ, Turnbull MH, Atkin OK.**
1005 **2014.** Canopy position affects the relationships between leaf respiration and associated traits
1006 in a tropical rainforest in Far North Queensland. *Tree Physiology* 34: 564-584.
- 1007 **Wilson KB, Baldocchi DD, Hanson PJ. 2000.** Spatial and seasonal variability of
1008 photosynthetic parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree*
1009 *Physiology* 20: 565–578.
- 1010 **Wright IJ, Reich PB, Cornelissen JH, Falster DS, Groom PK, Hikosaka K, Lee W, Lusk**
1011 **CH, Niinemets Ü, Oleksyn J et al. 2005.** Modulation of leaf economic traits and trait
1012 relationships by climate. *Global Ecology and Biogeography* 14: 411–421.
- 1013 **Wright SJ, Kitajima K, Kraft NJ, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling**
1014 **JW, Davies SJ, Díaz S et al. 2010.** Functional traits and the growth-mortality trade-off in
1015 tropical trees. *Ecology* 91: 3664–3674.
- 1016 **Wullschleger SD. 1993.** Biochemical limitations to carbon assimilation in C3 plants—a
1017 retrospective analysis of the A/Ci curves from 109 species. *Journal of Experimental Botany* 44:
1018 907.
- 1019 **Xu C, Fisher R, Wullschleger SD, Wilson CJ, Cai M, McDowell NG. 2012.** Toward a
1020 mechanistic modeling of nitrogen limitation on vegetation dynamics. *PloS one* 7: e37914.
- 1021 **Ziehn T, Knorr W, Scholze M. 2011.** Investigating spatial differentiation of model parameters
1022 in a carbon cycle data assimilation system. *Global Biogeochemical Cycles* 25: GB2021.

1023

1024 **Supporting Information**

1025

1026 Additional supporting information may be found in the online version of this article.

1027

1028 Fig. S1: Climatic space covered by this study shown by density hexagons.

1029 Fig. S2: Residuals ($V_{\text{cmax}} - \hat{V}_{\text{cmax}}$) shown as a function of a moisture index and elevation.

1030 Fig. S3: Residuals ($V_{\text{cmax}} - \hat{V}_{\text{cmax}}$) shown as a function of the number annual growing degree

1031 days above $> 0^{\circ}\text{C}$ and $> 5^{\circ}\text{C}$.

1032 Fig. S4: Fitted $R_{\text{day}}:V_{\text{cmax}}$ ratio (a) and (b) R_{day} as a function of leaf temperature using the
1033 Badger & Collatz (1977) parameters.
1034 Fig. S5: Fitted $R_{\text{day}}:V_{\text{cmax}}$ ratio (a) and (b) R_{day} as a function of leaf temperature using the
1035 Crous *et al.* (2013) parameters.

1036 TABLES

1037 **Table 1:** List of the data sets, site locations, vegetation types and associated references used in this study.**Commented [K4]:** Shouldn't this need to add up to the 1318 species?

Dataset	Site	Longitude	Latitude	References	Vegetation type
Ellsworth/Crous (51 species)	Aspen FACE, WI, USA	45.68	-89.63	Ellsworth <i>et al.</i> , (2004)	Temperate broadleaf deciduous forest
	Blue Mountains, NSW, Australia	-33.71	150.55	Ellsworth <i>et al.</i> , (2015)	Open eucalypt forest
	Cape Tribulation crane site, QLD, Australia	-16.10	145.45	Unpublished	Lowland tropical rainforest
	Carolina beach, NC, USA	34.05	-77.91	Unpublished	Temperate evergreen forest
	Carolina Lake, NC, USA	35.90	-79.09	Ellsworth <i>et al.</i> , (2004)	Temperate needle-leaved deciduous forest
	Cedar Creek LTER, USA	45.41	-93.19	Crous <i>et al.</i> , (2010)	Temperate savanna
	Cocoparra National Park, NSW, Australia	-34.17	146.23	Unpublished	<i>Callitris</i> pine woodland
	Driftway Cumberland Plain, Richmond, NSW, Australia	-33.62	150.74	Ellsworth <i>et al.</i> , (2015)	Open eucalypt forest
	Duke Forest, NC, USA	35.97	-79.10	Ellsworth <i>et al.</i> , (2004); Ellsworth <i>et al.</i> , (2012)	Temperate evergreen forest
	Endla bog, Endla, ESTONIA	58.86	26.17	Niinemets <i>et al.</i> (2001)	Boreal evergreen bog
	Hawkesbury, Richmond, NSW, Australia	-33.61	150.74	Crous <i>et al.</i> , (2013); Ellsworth <i>et al.</i> , (2015)	Open eucalypt forest
	Illawarra, Robertson, NSW, Australia	-34.62	150.71	Ellsworth <i>et al.</i> , (2015)	Wet sclerophyll forest
	Kuring-Gai National Park (Murrua Track), NSW, Australia	-33.69	151.14	Unpublished	Open eucalypt forest
	La Sueur National Park, WA, Australia	-30.19	115.14	Ellsworth <i>et al.</i> , (2015)	Kwongan woodland
	Nevada Test Site, NV, USA	36.77	-115.97	Ellsworth <i>et al.</i> , (2004)	Mojave desert
	Saginaw forest, MI, USA	42.27	-83.81	Unpublished	Temperate broadleaf deciduous forest
	UMBS Pellston, MI, USA	45.56	-84.72	Unpublished	Temperate broadleaf deciduous forest

	Mill Haft, Staffordshire, UK	52.80	2.30	Unpublished	Temperate broadleaf deciduous forest
JACARE (366 species)	Allpahuayo, Loreto, Peru (~100 m asl)	-3.95	-73.44	Atkins <i>et al.</i> , 2015; Malhi <i>et al.</i> , unpublished.	Humid Amazonian lowland forest
	Cuzco Amazonico, Peru	-3.37	-72.97	Malhi <i>et al.</i> , 2014; Anderson <i>et al.</i> , 2009	Forests over alluvial terrain
	Esperanza, Peru	-2.48	-71.97	Girardin <i>et al.</i> , 2014a, b	Upper limit of the cloud forest
	Jenaro Herrera, Peru	-4.88	-73.63	del Aguila-Pasquel <i>et al.</i> , 2014	Humid Amazonian lowland forest
	San Pedro, Peru	-6.54	-77.71	Huasco <i>et al.</i> , 2014	Cloud forest
	Sucusari, Peru	-3.25	-72.91	Atkins <i>et al.</i> , 2015	Humid Amazonian lowland forest
	Tambopata, Peru	-13.02	-69.60	Huasco <i>et al.</i> , 2014	Humid Amazonian lowland forest
	Trocha Union, Peru	-13.03	-71.49	Huasco <i>et al.</i> , 2014	Montane cloud forest
	Wayquecha, Peru	-13.12	-71.58	Girardin <i>et al.</i> , 2014a, b	Upper limit of the cloud forest
Togashi (51 species)	Great Western Woodland, WA, Australia	-30.25	-30.25	Unpublished	Temperate eucalyptus woodland
	Robson Creek, QLD, Australia	-17.25	145.75	Unpublished	Tropical rainforest
TROBIT (44 species)	Asukese, Ghana	7.14	-2.45	Domingues <i>et al.</i> (2010)	Humid tropical lowland forest
	Bissiga, Burkina Faso	12.73	-1.16	Domingues <i>et al.</i> (2010)	Tropical woody savanna
	Bissiga, Burkina Faso	12.73	-1.17	Domingues <i>et al.</i> (2010)	Tropical woody savanna
	Boabeng-Fiema, Ghana	7.71	-1.69	Domingues <i>et al.</i> (2010)	Seasonal tropical forest
	Dano, Burkina Faso	10.94	-3.15	Domingues <i>et al.</i> (2010)	Open tropical savanna
	Hombori, Mali	15.34	-1.47	Domingues <i>et al.</i> (2010)	Dry grass savanna
	Kogyae, Ghana	7.30	-1.18	Domingues <i>et al.</i> (2010)	Tropical woody savanna
Serbin (21 species)	Coachella Valley Agricultural Research Station, CA, USA	33.52	-116.16	Serbin <i>et al.</i> , (2015)	Vineyard and date palm
	Loma Ridge Coastal Sage-scrub EC site, CA, USA	33.73	-117.70	Unpublished	Coastal sage-scrub

	Sierra Mixed Conifer EC site, CA, USA	37.07	-119.20	Unpublished	Mixed conifer/broadleaf forest
	San Joaquin Experimental Range, CA, USA	37.08	-119.73	Unpublished	Semi-arid woodland
	San Jacinto James Reserve EC tower site, CA, USA	33.81	-116.77	Unpublished	Mixed conifer/broadleaf forest
	UW-Madison Arboretum, WI, USA	43.04	-89.43	Unpublished	Temperate broadleaf deciduous forest
Domingues (24 species)	Tapajós, Brazil	-3.75	-56.25	Domingues <i>et al.</i> , (2005)	Humid Amazonian lowland forest
Niinemets (3 species)	Ülenurme, Estonia	58.30	26.70	Niinemets (1998)	Temperate broadleaf deciduous forest
Rogers (7 species)	Barrow Environmental Observatory, Barrow, AK, USA	71.32	156.62	Unpublished	Tundra
Tarvainen (1 species)	Skogaryd, Sweden	58.23	12.09	Tarvainen <i>et al.</i> , (2013)	Hemi-boreal coniferous forest

1038

1039

1040 **Table 2:** Three sets of temperature dependencies for the Michaelis constant for CO₂, K_c ($\mu\text{mol mol}^{-1}$) and the Michaelis constant for O₂, K_o (mmol
 1041 mol⁻¹) and the CO₂ compensation point, Γ^* ($\mu\text{mol mol}^{-1}$). T_k is the leaf temperature in Kelvin, R is universal gas constant (8.314 J mol⁻¹ K⁻¹) and
 1042 O_i is the intercellular concentrations of O₂ (210 mmol mol⁻¹).

Reference	Badger and Collatz (1977)	Bernacchi et al. (2001)	Crous et al. (2013)
Environment	<i>in vivo</i>	<i>in vivo</i>	<i>in vitro</i>
Species	Bracted orache (<i>Atriplex glabriuscula</i>)	Tobacco (<i>Nicotiana tabacum</i>)	Tasmanian blue gum (<i>Eucalyptus globulus</i>)
K_c	If $T_k > 288.15$: $460 \cdot \exp\left(\frac{59536(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right)$ else if $T_k < 288.15$: $920 \cdot \exp\left(\frac{10970(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right)$	$404.9 \cdot \exp\left(\frac{79403(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right)$	Same as Bernacchi <i>et al.</i> (2001)
K_o	$330 \cdot \exp\left(\frac{35948(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right)$	$278.4 \cdot \exp\left(\frac{36380(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right)$	Same as Bernacchi <i>et al.</i> (2001)
Γ^*	$\frac{K_c \cdot O_i \cdot 0.21}{2 \cdot K_o}$	$42.75 \cdot \exp\left(\frac{37830(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right)$	$38.892 \cdot \exp\left(\frac{20437(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right)$

1043

1044

